

Effect of Exploitation on the Limpet *Lottia gigantea*: A Field Study in Baja California (México) and California (U.S.A.)¹

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ABSTRACT: Specimens of *Lottia gigantea* (Sowerby) from intertidal populations, artisanal catches, and shell middens were obtained from 1985 to 1988 at 11 sites along the Pacific coasts of Baja California (México) and California (U.S.A.). A scaled rating system of 0–4 was used to describe the amount of intertidal exploitation associated with visiting patterns of gatherers, accessibility, and site topography. Maximum and mean size of intertidal populations and artisanal catches decreased along a gradient of increasing exploitation. Mean size was significantly different between catches and the corresponding intertidal population. Mean size of specimens in older middens was significantly larger than in a recent midden. Measurements at the most inaccessible site immediately after the exceptional extratropical winter storm that swept the California coast on 17–18 January 1988 showed that the storm had removed larger specimens approximating exploitation measuring 1–2 on our scale. Intertidal gathering occurs or has occurred unless it is physically prevented by topography, distance, or some kind of restriction of access. Ecological implications of exploitation were explored utilizing the conceptual model proposed by Catterall and Poiner for assessing potential impact of traditional shell gathering on intertidal molluscs. The model suggests that size at maturity of this species and its pelagic larval stage may prevent depletion by harvesting.

MOST INTERTIDAL HABITATS worldwide are exploited by artisanal harvesters using simple tools. The production, which is seldom included in official fisheries statistics, is either consumed by individual gatherers or family groups or sold in small-scale trade (Durán et al. 1987). Artisanal harvesting includes a variety of organisms such as lugworms, limpets, and gastropods. The effect of human exploitation relative to natural processes in populations of harvested marine invertebrates is an

issue of substantial interest in contemporary ecology and conservation biology (Catterall and Poiner 1987).

Studies of the role of humans as predators in the intertidal has focused largely on population density and size structure of prey at harvested and nonharvested sites; some studies have analyzed the implications of harvesting in terms of biomass and gonad outputs (Branch 1975, Blake 1979, McLachlan and Lombard 1981). The effects of human predation on intertidal populations have also been analyzed in terms of community ecology; the concepts of top carnivore and keystone species (Paine 1966) as well as the intermediate disturbance hypothesis (Connell 1978) have been employed to explain profound changes in species richness, community structure, and size structure of component species at sites with and without human predation (Moreno et al. 1984, Hockey and Bosman 1986).

On Baja California shores, several species

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of invertebrates are exposed to artisanal exploitation (Pombo 1990). Most species are removed for direct human consumption: mussel (*Mytilus californianus* Conrad); clams (mainly Pismo clam, *Tivela stultorum* Mawe); abalone (*Haliotis* spp.); keyhole limpet (*Megathura crenulata* [Sowerby]); snail (*Astraea undosa* [Wood]); owl limpet (*Lottia gigantea* [Sowerby]); and gooseneck barnacle or leaf barnacle (*Pollicipes polymerus* Sowerby). Abalone are also collected, as juveniles, for ornamental purposes. The ghost shrimp (*Callinassa californiensis* Dana) is used as fish bait. Chitons (*Stenoplax* spp.), keyhole limpet, black abalone (*Haliotis cracherodii* Leach), snail, and owl limpet are used as bait in spiny lobster traps. Most species come from the rocky intertidal; snail and all abalone except black are extracted from the sublittoral, and ghost shrimp and clams from soft bottoms.

The owl limpet, *Lottia gigantea*, is the largest limpet in North America. It lives on exposed and semiexposed rocks and cliffs in high middle and upper littoral zones from northern Washington to central Baja California (Ricketts and Calvin 1939, Stimson 1973, Lindberg and Wright 1985, Wright 1989). Zedler (1976, 1978) found lower abundance of larger individuals of *L. gigantea* in areas of greater human use than at the Cabrillo National Monument, Point Loma, California, where collecting is restricted. Ghazanshahi et al. (1983) included *L. gigantea* in the list of species likely to be affected by public use.

Our data relate different degrees of intertidal exploitation to the sizes of individuals in populations of *L. gigantea* in 11 localities along the Pacific coasts of Baja California (México) and California (U.S.A.). We also investigated the effect of the history of exploitation at a site, the effect of human exploitation relative to physical disturbance by strong storm-generated waves, and the ecological implications of exploitation.

MATERIALS AND METHODS

Specimens of *Lottia gigantea* from intertidal populations, artisanal catches, and abo-

iginal shell middens were collected during field studies conducted from 1985 to 1988 at 11 sites along the Pacific coasts of Baja California (México) and California (U.S.A.) (Figure 1). A rank scale of 0–4 was used to describe the degree of intertidal exploitation for each site. Criteria used to rate the intertidal gathering were as follows: (1) gatherers' visiting pattern to the intertidal during the 3-yr period in which the study was conducted and in the past, according to reports of local dwellers; (2) several features of the sites that could explain degrees of exploitation (topography, distance from mainland or major human settlements, habits of consumption of intertidal species by local people, existence and length of protective management programs).

Individual elements of the scaled intertidal gathering rating system of 0–4 were assigned as follows:

Rating 0: Sites where intertidal gathering never occurred because of steep topography that physically prevents access (La Bufadora) or where it was certifiably absent for approximately the last 30 yr because of protective management (all sites at Santa Cruz Island, Channel Islands).

Rating 1: (1) Lobera, where the local oyster farm cooperative has banned intertidal gathering since 1984 to promote abalone recovery; only two abalone harvesting seasons have been allowed since then; (2) Isla Guadalupe, where gathering is rare because the site is isolated from the mainland and there are no fishing settlements nearby. A small number of military personnel at an outpost collect abalone during very low tides that coincide with official holidays.

Rating 2: (1) Chorera, a site protected by the local oyster farm cooperative since 1985. Only five resident family groups of fishermen are allowed in the area. However, their visits are frequent, because of feeding habits; gathering of several species, mostly abalone, was confirmed in the field; (2) El Campito, where access is free but people are seldom observed (its vicinity to Chorera, a protected area, may deter visitors).

Rating 3: Cantiles, a site open to the public but relatively inaccessible (5 km from a

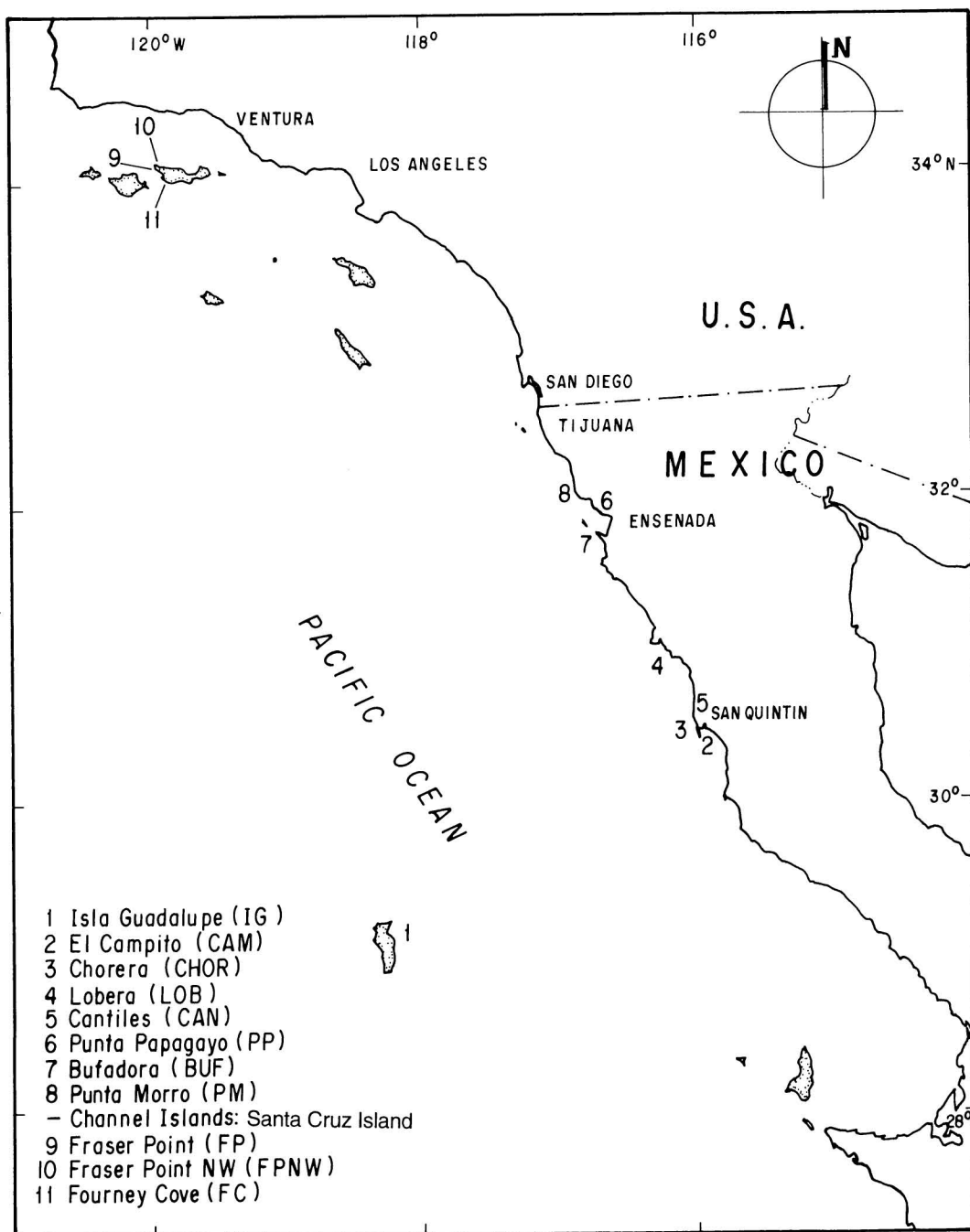


FIGURE 1. The study sites.

major town; unpaved roads); gatherers arrive irregularly, usually on major holidays.

Rating 4: The highest degree of exploitation was assigned to Punta Papagayo and Punta Morro, where numbers of gatherers are observed all year round, almost daily. Both sites have free access, are located 1 km from a major city (Ensenada, B. C., México), and have paved roads.

In all the intertidal samples, except those from La Bufadora, all individuals of *L. gigantea* detected along a randomly chosen strip 2 m wide across the intertidal were collected, and shell length (longest axis to the nearest mm) was measured in the laboratory. Specimens were frozen to preserve them for later determination of growth rate, sex, and maturity, as part of more extensive studies (Pombo 1990).

At La Bufadora, inaccessibility of the wall occupied by *L. gigantea* forced us to make indirect measurements. One person dangled a ruler on the wall with the aid of a sport fishing rod while another person took pictures from the opposite side. The entire wall was covered in bands one film frame high. A 200-mm telephoto lens and ASA 400 slide film were employed. The length of the specimens was calculated by converting the dimensions in projected images. The error of the method was calculated by taking pictures of the same ruler placed by an array of 48 limpet shells of known length, at five different distances equivalent to those in the field. The measurement error, using 95% confidence interval was 0.48 ± 0.89 mm.

The number and size of limpets collected by present-day artisanal harvesters was recorded and the catches were returned to the harvesters.

To explore intertidal exploitation in the past, specimens of *L. gigantea* were measured at two Indian shell middens 3 km apart on Santa Cruz Island (California, U.S.A.) where the stratigraphic sequence was finely dated by Glassow (1980): Fraser Point (superficial, mussel-dominated strata dated 280 ± 150 yr B.P.); Fournery Cove (4 m deep; the last abalone-dominated strata, dated 2310 ± 150 yr B.P.).

The magnitude of the effect of harvest

by gatherers was compared with the effect caused by storm waves. A second set of indirect measurements was carried out at La Bufadora immediately after the exceptional extratropical winter storm that swept the California coast on 17–18 January 1988. In the results, Bufadora BS (BUF-BS) and Bufadora AS (BUF-AS) respectively indicate data obtained before and after the January 1988 storm.

To compare shell length, a parametric analysis of variance (ANOVA) of unbalanced design was applied for more than two samples. A Student-Newman-Keul's multiple range test at $\alpha = 0.05$ (Sokal and Rohlf 1979) was used for post-hoc comparisons of population means in the ANOVA model when significant among-population differences ($P < 0.05$) were detected. For comparisons of two samples outside the ANOVA model, a two-tailed *t*-test at $\alpha = 0.05$ was performed.

Ecological implications of exploitation were explored through the conceptual model proposed by Catterall and Poiner (1987) for assessing the potential impact of traditional shell gathering on intertidal molluscs. The model uses life history and habitat information to predict the extent to which a given intertidal shellfish population would be either susceptible to depletion or resilient.

RESULTS

Size Structure at Field Sampling Sites

In the intertidal populations the size of individuals ranged from 102 to 17 mm (Table 1). Mean size was significantly different among sites ($F = 92.647$; $P < 0.05$). The multiple range test yielded five groups: (1) values higher than 50 mm (Bufadora BS); (2) values between 45 and 50 mm (Lobera, Fraser Point, and Isla Guadalupe); (3) values between 40 and 45 mm (Chorera and Fraser Point NW); (4) values between 30 and 40 mm (Cantiles); (5) values lower than 30 mm (Punta Papagayo and Punta Morro). The size of mature individuals ranged from 21 to 73 mm. The mean size of mature males varied

TABLE 1

SIZE RANGE (SR) (mm) AND MEAN SIZE (\bar{x}) (mm) OF *Lottia gigantea* IN SAMPLES FROM INTERTIDAL, CATCHES, AND MIDDENS AT 11 SITES WITH DIFFERENT DEGREES OF EXPLOITATION (DE)

SITE	DE	SAMPLE FROM		
		INTERTIDAL	CATCHES	MIDDENS
BUF-BS	0	SR = 102–30 \bar{x} = 55.0 \pm 13.7 <i>n</i> = 125		
BUF-AS, all data	0	SR = 107–32 \bar{x} = 50.9 \pm 14.6 <i>n</i> = 28		
BUF-AS, outlier removed	0	SR = 72–32 \bar{x} = 48.8 \pm 9.8 <i>n</i> = 27		
Channel Islands: Fraser Point	0	SR = 72–31 \bar{x} = 49.0 \pm 9.4 <i>n</i> = 61		SR = 62–26 \bar{x} = 39.9 \pm 6.9 <i>n</i> = 93
Fraser Point NW	0	SR = 67–28 \bar{x} = 42.5 \pm 8.7 <i>n</i> = 57		
Fourney Cove	0			SR = 68–26 \bar{x} = 50.3 \pm 7.2 <i>n</i> = 37
Lobera	1	SR = 75–29 \bar{x} = 49.3 \pm 7.6 <i>n</i> = 97		
Isla Guadalupe	1	SR = 78–17 \bar{x} = 48.7 \pm 13.9 <i>n</i> = 131	SR = 80–42 \bar{x} = 56.7 \pm 8.7 <i>n</i> = 66	
Chorera	2	SR = 57–28 \bar{x} = 43.9 \pm 6.1 <i>n</i> = 114		
El Campito	2		SR = 55–46 \bar{x} = 50.7 \pm 4.3 <i>n</i> = 90	
Cantiles	3	SR = 58–20 \bar{x} = 37.8 \pm 8.3 <i>n</i> = 60		
Punta Papagayo	4	SR = 44–20 \bar{x} = 29.7 \pm 6.2 <i>n</i> = 68	SR = 33–23 \bar{x} = 27.8 \pm 5.2 <i>n</i> = 119	
Punta Morro	4	SR = 49–18 \bar{x} = 28.4 \pm 6.8 <i>n</i> = 103		

between 47.0 \pm 8.3 and 31.4 \pm 6.5 mm; mean size of mature females varied between 52.2 \pm 6.5 and 31.2 \pm 6.4 mm. Sex ratio varied from 60% males and 40% females with none or few undetermined individuals at Chorera and Lobera to 26% males and 38% females with 64% undetermined individuals at Punta Morro.

The January 1988 winter storm caused

77.6% mortality at La Bufadora (125 organisms detected in 1987, 28 survivors after the storm). Mean size before and after the storm was not significantly different when all data were considered (t_{calc} = 1.355, P > 0.05) but was significantly different when a 107-mm specimen suspected to be a methodological outlier was removed from data (t_{calc} = 2.22, P < 0.05). Size range before and after the

storm also appeared similar considering all data after the storm but was quite reduced when the suspected outlier was removed.

In catches, size of individuals ranged from 80 to 23 mm. The average size of limpets in catches from each site was significantly different from that of limpets in the corresponding intertidal populations (Isla Guadalupe, $t_{\text{calc}} = 4.947$, $P < 0.05$; Punta Papagayo, $t_{\text{calc}} = 2.313$, $P < 0.05$). The smallest individuals in catches were always larger than the smallest individuals in the intertidal.

In the shell middens, the size of individuals ranged from 68 to 26 mm. Size range and

maximum size were similar in both middens. Mean size of the specimens found in the older strata (Fourney Cove) was significantly larger ($t_{\text{calc}} = 7.50$, $P < 0.05$) than in the more recent deposit (Fraser Point). At Fraser Point, mean size of individuals in the midden was significantly smaller than that of the current intertidal population ($t_{\text{calc}} = -2.709$, $P < 0.05$).

Effect of Harvesting

Mean size, maximum size, and size range of intertidal populations decreased along the exploitation gradient (Figure 2). Mean size in

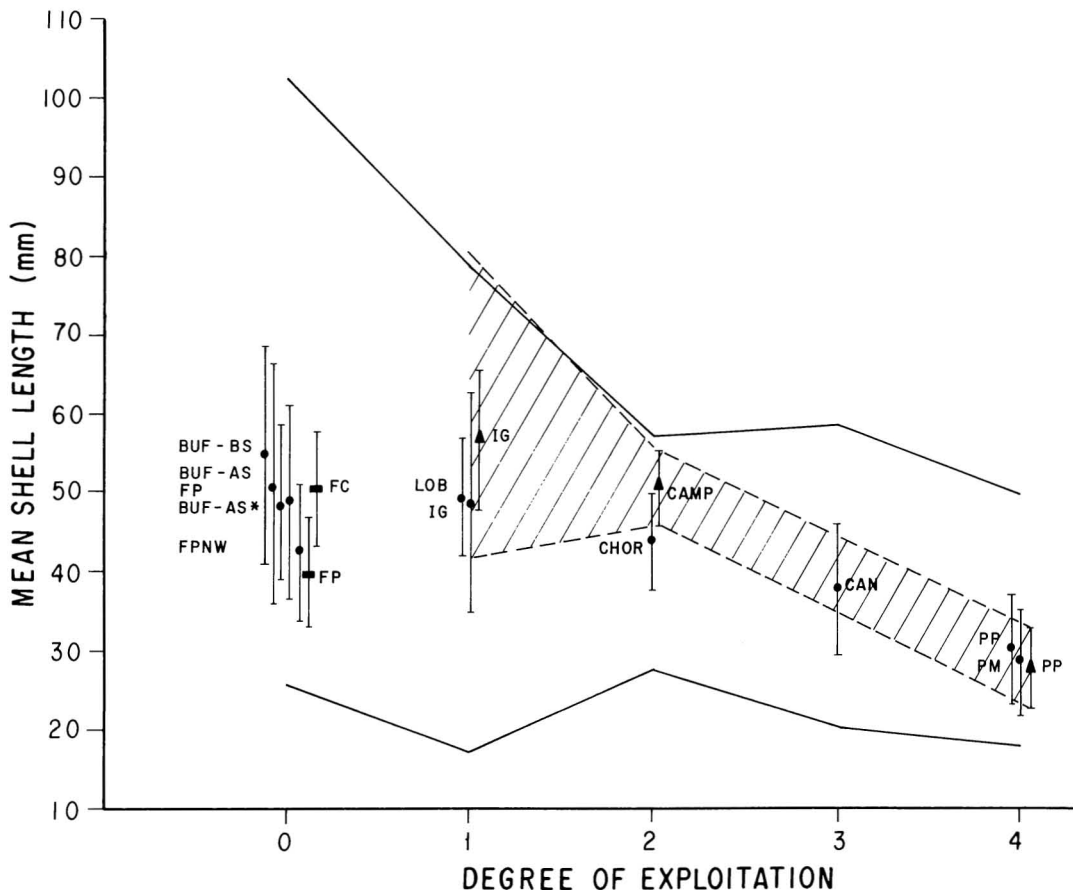


FIGURE 2. Mean size of *Lottia gigantea* from intertidal (circles), catches (triangles), and middens (rectangles) along the exploitation gradient, depicted within the limits of the size range of the intertidal population (solid lines) and catches (shaded area). Abbreviations for the sites as in Figure 1 and text; BUF-AS* indicates that the results were obtained at BUF-AS after the removal of the suspected outlier from data. At exploitation rating 0, limits are set according to BUF-AS values.

seven of the nine intertidal populations (Bufadora BS, Lobera, Isla Guadalupe, Chorera, Cantiles, Punta Papagayo, Punta Morro) decreased along a gradient of increased exploitation ($R^2 = 0.395$, $n = 589$). At Fraser Point and Fraser Point NW, mean size was smaller than expected at sites without exploitation, close to sizes found at sites with degree of exploitation ratings of 2–3 and 1–2, respectively. Mean size in artisanal catches also decreased along the exploitation gradient (Isla Guadalupe-El Campito-Punta Papagayo). Difference between mean size of catches and those of the corresponding intertidal populations was maximal (27 mm) at Isla Guadalupe, with a low amount of exploitation, and minimal (3.0 mm) at Punta Papagayo, with the highest exploitation.

Plotting of data from middens and Bufadora AS within the former scheme suggested that exploitation in the past was low at

Fourney Cove and more intense at Fraser Point (ratings of 1–2 and 3–4 in our scale, respectively) and that the storm had removed the larger specimens to a degree similar to an exploitation rating of 1–2 in our scale.

Ecological Implications of Exploitation

The analysis of life history and habitat information in the model proposed by Catterall and Poiner (1987) singled out two attributes that presumably make it unlikely that local populations of *L. gigantea* will be driven to extinction: their small size at maturity, and existence of a pelagic larval stage (Table 2). Other biological characteristics proposed by the model (intertidal burying, adjacent subtidal populations, benthic mobility) do not apply to *L. gigantea*, which only occurs on intertidal hard substrate and has limited mobility in the adult stage.

TABLE 2

BIOLOGICAL ATTRIBUTES CONSIDERED TO BE THE MORE IMPORTANT DETERMINANTS OF THE CONSEQUENCES OF TRADITIONAL GATHERING OF SHELLFISH POPULATIONS (CATTERALL AND POINER 1987) AND ITS ILLUSTRATION IN *L. gigantea*

ATTRIBUTE	MODEL STATEMENT	RESULTS
Size at maturity	If size at maturity is less than size detectable by gatherers, a population will always contain reproducing individuals.	Mature females (25.8 mm) and males (25.0 mm), close to the size of the smallest individuals in catches (23 mm) were registered in the study area.
Intertidal burying	If individuals large enough to be detectable have the opportunity to bury themselves within soft substrate, a refuge from predation or gathering can be attained.	<i>L. gigantea</i> only occurs on hard substrate (Stimson 1973).
Adjacent subtidal populations	If a local intertidal population is depleted, replenishment may be possible through recruitment of individuals from adjacent subtidal areas.	<i>L. gigantea</i> is strictly intertidal (Stimson 1973).
Benthic mobility	In species with partially subtidal distribution, if benthic stages are mobile, reproductive individuals may migrate into the exploited intertidal areas, providing an opportunity for local reproduction.	<i>L. gigantea</i> is intertidal and has limited mobility as adult (Stimson 1973).
Pelagic larvae	Irrespective of benthic migration of adults, if a species has a pelagic larval stage lasting long enough to permit settlement of larvae spawned by distant, unexploited populations, recruitment into exploited areas would continue as long as enough such populations remained.	<i>L. gigantea</i> has a planctonic larval stage. Duration of planctonic larval stage is unknown (Stimson 1973).

DISCUSSION

Since the publication of the pioneer paper by Branch (1975), there have been numerous demonstrations of the effect of exploitation on populations of intertidal invertebrates (Zedler 1976, 1978, Blake 1979, McLachlan and Lombard 1981, Moreno et al. 1984, 1986, Castilla and Durán 1985, Hockey and Bosman 1986, Oliva and Castilla 1986). Most comparisons were made between sites with and without exploitation, and the effect of the degree of exploitation has only been explored by Branch (1975) and Moreno et al. (1984).

Our procedure to rank levels of human activity in the intertidal is close to the procedure of Moreno et al. (1984) in considering proximity and size of settlements or fishing communities and existence and length of protection as reasonable predictors of intensity of human activity. Also, it is similar to the procedures of Beauchamps and Gowing (1982), Ghazanshahi et al. (1983), and Underwood and Kennelly (1990) in considering counts of people as a measure of public accessibility.

Our results, showing a reduction in population size range and a decrease of the mean size of specimens of *L. gigantea* along five different ratings of amount of intertidal exploitation, are similar to the results of several other studies. Moreno et al. (1984) reported a similar pattern in the exploitation of *Fissurella picta* (Gmelin) at four sites with different levels of human activity, and Oliva and Castilla (1986) reported reduced size of individuals and reduced abundance of *Fissurella crassa* Lamarck and *F. limbata* Sowerby at harvested versus nonharvested sites. Branch (1975) reported a reduction in average size and abundance of *Patella concolor* Krauss at 13 individual sites over a 5-yr period of increasing exploitation.

Our results also show that mean size in artisanal catches decreased along the exploitation gradient and that the difference between mean size in the catches and in the intertidal population becomes smaller as exploitation increases. The effect of exploitation was also evident comparing the smallest

size in the catches and in the intertidal population: as exploitation increases, both values became closer to each other (27-mm difference at Isla Guadalupe; 3-mm difference at Punta Papagayo).

These results convey that the decrease in mean size, as a descriptor of the effect of exploitation, is reinforced by the decrease in maximum size and size range of intertidal populations (Branch 1975). Our results suggest that at sites with heavy exploitation, the mean size of intertidal populations and catches may not demonstrate satisfactorily the selection of larger sizes by gatherers. In our results, the smallest individuals in the catches were always larger than the smallest individuals in the intertidal, suggesting that harvesters are size selective and preferentially take larger limpets even at sites where heavy exploitation has reduced the population size range. This is shown at Punta Papagayo (highest degree of exploitation) where the mean size of the catch was smaller than in the intertidal population, but selection of the larger individuals can be shown through difference between size range in the catches and in the intertidal population.

Consistent lack of specimens below 17 mm, both in intertidal populations and catches, suggests that the smallest individuals are hidden in inaccessible microhabitats or are inconspicuous (e.g., mussel beds, tufts of algae), which is the case for at least two species in the study area: juveniles of *Pachygrapsus crassipes* Randall are only found among tubes of the sand castle polychaete, *Phragmatopoma californica* (Fewkes) (Escofet et al. 1992); those of black abalone, beneath tufts of *Pelvetia compressa* (C. Agardh), in Bahía San Quintín (pers. obs.).

The decrease in mean size of individuals in intertidal populations was consistent along the following sequence: Bufadora BS-Lobera-Isla Guadalupe-Chorera-Cantiles-Punta Morro-Punta Papagayo. Mean size of individuals at two sites remained unexplained under the exploitation hypothesis: Fraser Point and Fraser Point NW, where sizes were smaller than expected after 20 yr of protective management.

For Fraser Point, we propose that the

major factor for size reduction is wave exposure, a physical stress that may limit maximum size of mobile invertebrates either by selective mortality of the larger individuals or by decreased access to food (Judge 1988). The latter hypothesis is supported by the slower individual growth of *L. gigantea* documented at Fraser Point (Pombo 1990), although our data from La Bufadora suggest that larger individuals are selectively affected by storms. Also, comparison between midden and intertidal samples shows that a recovery has occurred at Fraser Point because of protective management, but that recovery of size cannot surpass the limits imposed by the physical stress. This can also be supported by data from Bufadora AS, where mean size was close to that at Fraser Point.

For Fraser Point NW we propose that the presence of abalone might be a source of stress that imposes physical barriers for grazing. Although they do not compete with limpets for food, abalone may limit the availability of substrata. Currently, the intertidal assemblage at Fraser Point NW is unusual; abalone were once common on California rocky shores (Ricketts and Calvin 1939) but have been heavily exploited at accessible sites. Our results suggest that the protective management at Fraser Point NW allowed the recovery of the original biological assemblage for semiexposed rocky shores, including abalone, and that this may have resulted in restriction of the *L. gigantea* population or reduction in the growth rates of individuals.

Data obtained at the middens can be linked with the general process of human gathering in the intertidal (Reinman 1954, McKusic and Warren 1959, Meighan 1959, Rozaire 1967, Orr 1968, King 1971, Swalding 1976, Glassow 1980, Tellez 1985). Assuming that a shift in food preferences of aboriginal people occurred after local depletion of populations of the preferred species (Simenstad et al. 1978), we propose that: (1) species assemblage and larger sizes of *L. gigantea* found in the Fourny Cove midden are indicative of the end of an intense exploitation of abalone and early exploitation of other species, including *L. gigantea*; and (2) composition and smaller sizes of *L. gi-*

gantea found in the Fraser Point midden denote a later stage, where abalone were no longer abundant, and extraction of mussels, limpets, and other species began to be more intense.

The relative effect of natural processes can be masked where exploitation occurs. In that sense, La Bufadora emerges as a natural experiment. Because of extreme inaccessibility, exploitation is absolutely blocked, and only natural factors affect the population; had exploitation occurred there, the effect of physical disturbance would not have been visible. Before the 1988 storm, the site had specimens of *L. gigantea* as large as those reported 50 yr ago (Ricketts and Calvin 1939). After the storm (especially when the suspected outlier was removed from the analysis), the average size of individuals was significantly smaller, demonstrating that physical disturbance is also size selective (Judge 1988); its effects on size, at least for the exceptional January 1988 storm, which had the highest waves in 50 yr (Seymour et al. 1989), are comparable with exploitation rating 1–2 in our scale.

Populations of *L. gigantea* are subject to heavy exploitation along the California coast, yet have persisted. An analysis of the life history and natural history of this limpet using the factors proposed by Catterall and Poiner (1987) suggests that two factors in particular may be responsible for the species persistence: the small size at maturity and the pelagic dispersal stage. The occurrence of mature females and males at sizes close to those of the smallest individuals in catches suggests that maturity can be attained before individuals are noticeable or valuable to harvesters. The existence of a pelagic larval stage and the associated capability for dispersal may not be important in the persistence of populations if the refuges for the species are few or far from the sites of intense harvesting.

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